Habitat fragmentation influences nestling growth in Mediterranean blue and great tits

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Abstract

In patchy forest areas, the size of the forest patch where birds breed has a strong influence on their breeding success. However, the proximate effects contributing to lowering the breeding success in small forest patches remain unclear; and a shortage of crucial resources in those forest patches has been suggested to account in some degree for this failure. With the aim to further investigate this issue, we have monitored the breeding cycle of blue and great tits in three 'large' forest patches (ranging between 26.5-29.6 ha) and twelve 'small' forest patches (ranging between 1.1-2.1 ha) in a Mediterranean area in central Spain, during three years (2011-2013). We also recorded the nestling diet inside the nest-boxes with the aid of handy-cams. Only males significantly differed between forest patch size categories; being on average younger and with better body condition in small patches for great and blue tits respectively. Reproductive traits did not vary between forest patch size categories, but the body condition of blue tit nestlings and the size of great tit nestlings did, being significantly better and larger respectively in large forest patches. The recruitment rate of blue tit nestlings was also higher in large patches. Regarding nestling diet, blue tits did not differ but great tits did, delivering a larger amount of caterpillars in large forest patches. Most variation in the reproductive traits occurred between years, probably due to annual differences in environmental conditions. This study suggests that food supply could be limiting the breeding success of birds above all in small patches, but also in large patches under particular environmental conditions.

Additional keywords: Forest patch; feeding behavior; recruitment; nestling diet; body condition.

1. Introduction

Habitat fragmentation is one of the major threats that forest biodiversity faces (Laurance, 2010; Amos et al., 2013; Bregman et al., 2014), and its effects have been widely studied in forest birds (Fahrig, 2003). The ultimate effect of habitat fragmentation is the decline of bird species richness and population abundances (Moller, 1987; Debinski and Holt, 2000; Boulinier et al., 2001). These numerical responses may stem, at least in part, in demographic changes, i.e. proximate effects given at a regional-scale (Lampila et al., 2005). However, the mechanisms underlying these proximate effects remain unclear, and it is of vital importance to light them in the sake of conservation biology (Boulinier et al., 2001; Le Tortorec et al., 2012). One feature that affects the breeding success of birds, is the size of the forest patch where they breed (Paton, 1995; Hinsley et al., 1999, 2009; Shochat et al., 2001; Loman, 2003; Zitsque et al., 2011, but see Nour et al., 1998), and a reduction of crucial resources in small forest patches has been suggested to be a responsible cause (Kuitunen and Makinen, 1993; Tremblay et al., 2005; Hinam and Clair, 2008).

In this regard, food supply could be a crucial resource limiting the breeding success of birds in small forest patches, as it is one of the most important limiting factors affecting life-history in birds (Lack, 1968; Martin, 1987; but see Martin, 1995). Food supply could be compromised in small forest patches just because their small surface area (Moller, 1991); but also because in small forest patches the proportion of forest edges increases (Helzer and Jelinski, 1999), which harsh the environmental conditions (Zanette et al., 2000) and may drive to a decrease in the amount of invertebrates (Didham et al., 1996; Burke and Nol, 1998). Furthermore, the process of habitat fragmentation typically implies

66 degradation, which changes the structure of the remaining habitat (Hinsley et al., 1999;
67 Fahrig, 2003). These changes in the vegetation structure usually involve microclimate
68 alterations too; which apart from its direct effects on the abundance of invertebrates, it
69 could promote a change in the composition of the vegetation which could also alter the
70 composition of invertebrates (Cramp and Perrins, 1993; Laurance et al., 2002). In addition,
71 for altricial bird species, breed in a small forest patch could be challenging due to they are
72 'central-place foragers', as they are attached to a fixed point when they breed, their nests
73 (Tremblay et al., 2005). If they are not able to cope with the food demand of their broods
74 within the patch, they will be forced to travel longer distances to reach other foraging
75 patches, crossing unsuitable foraging habitats, which will limit their feeding rate (Bruun
76 and Smith, 2003). In other cases, in landscapes containing little habitat, the distance
77 between forest patches may exceed a species gap-crossing tolerance, constraining the size
78 of the home ranges and limiting the availability of resources (Desrochers and Hannon,
79 1997). The ultimate effect of both scenarios is a reduction of the breeding success (Frey-
80 Roos et al., 1995; Hinsley, 2000).

81 The aim of the present study was to test whether there is an effect of the forest patch
82 size on the breeding performance of two populations of blue (*Cyanistes caeruleus*) and
83 great tits (*Parus major*). To do this, we studied the breeding performance of these two
84 species of tits in a fragmented landscape in central Spain during three years. Both species
85 are ideal to study this topic as they need an enormous supply of food when they breed. For
86 example great tits while feeding their chicks made up to 700 feeding visits per day, and
87 blue tits even more (Perrins, 1991). Because of this, it is crucial for tits to match the
88 maximum food demand period of their chicks with the food peak in the forest (Naef-

Daenzer and Keller, 1999; Matthysen et al., 2011); when they do not achieve this match, their reproductive success can decrease (Svensson and Nilsson, 1995; Naef-Daenzer et al., 2001; Tremblay et al., 2003). We hypothesized that in small patches the breeding performance will be worse (Moller, 1991; Riddington and Gosler, 1995), and predict that the lack of resources in small patches will be an important responsible factor, concretely food supply (Burke and Nol, 1998; Zanette et al., 2000; Razeng and Watson, 2014).

2. Material and Methods

2.1. Study area

The present study was conducted in the locality of San Pablo de los Montes situated in Montes de Toledo (39°32′44″N, 4°19′41″W; Toledo, central Spain). This region presents continental Mediterranean climate, characterized by pronounced summer droughts and a high daily thermal oscillation, with mean annual rainfall of 700-800 mm. The landscape of this area has suffered an intense fragmentation due to human activities, mainly agriculture and deforestation for raising cattle, as occurs in other regions of the Mediterranean basin (Blondel and Aronson, 1999). As a consequence, deciduous woodlands, considered the most suitable breeding habitat for tits in this region (Atiénzar et al., 2012), are scattered and patched in a matrix of less suitable habitat, mainly Mediterranean scrubland with low tree cover and pastureland. Our study area consisted of fifteen oak (*Quercus pyrenaica*) forest patches: three '*large*' patches ranging between 26.5 and 29.6 ha, and twelve '*small*' patches ranging between 1.1 and 2.1 ha, separated from each other by a mean distance of 4.23 km (range 0.53 - 9.84 km). Both oak forest patch size categories present a similar habitat

111 structure, with the oak as dominant plant accompanied by its typical shrub courtship:
112 common hawthorn (*Crataegus monogyna*), elmleaf blackberry (*Rubus ulmifolius*), terebinth
113 (*Pistacia terebinthus*), and common broom (*Cytisus scoparius*). Large patches were
114 provided with 80 wood nest-boxes (internal dimensions: 12 x 11.5 x 16.5 cm.) and small
115 ones with 5 wood nest-boxes; separated from each other by at least 30 m. All nestboxes
116 were hung on the branches of oak trees at a height of 2.5-3 metres and oriented towards the
117 south. They were protected from predators (mustelids, woodpeckers) with wire mesh and a
118 polyvinyl chloride (PVC) pipe (length: 50–70 mm, diameter: 40 mm) fixed to the hole-
119 entrance. Because of this protection, the main predator in our study area was the ladder
120 snake (*Rhinechis scalaris*), a very common species in the area (Salvador and Pleguezuelos,
121 2002).
122
123 *2.2. Field work*
124 During the 2011-2013 breeding seasons (day 1= April 1), nest-boxes were
125 frequently inspected to obtain the basic reproductive parameters of our tit population, such
126 as laying date (the day of laying the first egg of the clutch), clutch size, hatching date and
127 brood size. Body condition, size and age of parents were compared between patch size
128 categories because these variables are indicators of status and thus of dominance over
129 resources (Gosler, 1997; Stahl et al., 2001). To do this, parents were trapped and ringed
130 while feeding their nestlings (8-9 days old). The tarsus length of birds was measured with a
131 digital calliper to the nearest 0.01 mm; the body weight was measured with an electronic
132 balance (0.01 g) and the age of parents (yearling or older) was noted according to plumage
133 characteristics. Due to technical difficulties, adult great tits in 2011 were not trapped.

Nestlings were ringed, measured and weighted when they were 13 days old, and mean values per brood were taken in the analyses. Tarsus length was employed as a surrogate of body size, and the weight analyses were corrected by the tarsus length (added as a covariate) to consider the body condition of birds. Nest-boxes were also visited on day 22 to assess the number of chicks fledged. We assumed that all chicks have fledged when we did not find any chick dead inside the nest-boxes. Hatching success was calculated as the ratio between the number of nestlings hatched and the clutch size; and fledgling success was calculated as the ratio between nestlings fledged and hatched. To assess the breeding performance of each tit pair, seven variables were used (laying date, clutch size, hatching success, fledgling success, nestling body condition, nestling size and fledgling recruitment). Fledgling recruitment was estimated by noting, for each yearling that we recaptured (i.e. that was born in the study area); the forest patch ID where it was breeding and the forest patch ID where it was born. Through this way, we could estimate the percentage of recruitments that were born in large or small patches and the percentage of them that achieved to breed in large or small patches the next year. Apart from the seven breeding variables mentioned above, we also estimated the nest-box occupation rate and the breeding density to increase the comprehensive approach of this study. Nest-box occupation rate was obtained for each species and year as the ratio between occupied nest-boxes and total availability of them in each forest patch. We also calculated the density of great and blue tits in each breeding territory as the number of tit breeding pairs in a radius of 75 m around each occupied nest-box with the aid of Quantum GIS 2.0.1, as it is an important trait influencing breeding performance and recruitment rate (Both, 1998; Both et al., 1999).

157 *2.3. Feeding rate and Nestling diet*

158 To evaluate potential differences in the breeding performance between patch size
159 categories, nestling diet was filmed by placing an infrared handy-cam (Sony DCR-SR290E-
160 like) in an adapted nest box when nestlings were 11 days old (see García-Navas and Sanz,
161 2011, for details); that is, when nestling food requirements are maximum (Naef-Daenzer
162 and Keller, 1999). All filming sessions were carried out during the first hours of the day
163 and in similar weather conditions. First hour of video of each recording was discarded to
164 allow parents to habituate to the disturbance that the video camera installation entails. The
165 second hour of recording was analysed frame by frame using the software package Adobe
166 Premiere Elements 7.0. In a previous study performed in a nearby area, it was confirmed
167 that an hour is representative of the feeding behaviour in these species (García-Navas and
168 Sanz, 2012). A total of 247 film recordings were analysed, 186 belonged to blue tits (131 in
169 large patches and 55 in small ones. Table S2) and 61 from great tits (29 in large patches and
170 32 in small patches. Table S2). For each recording, we combined the number of feeding
171 events of each adult. Thus, the number of feeding events per hour was considered as a
172 surrogate of parental provisioning effort (hereafter 'feeding rate'). Diet of nestlings was
173 estimated from identified preys of 6,017 feeding trips: 5,037 belonging to blue tits and 980
174 to great tits. Food items were firstly classified in two main trophic categories: Lepidoptera
175 larvae (caterpillars) and "others". We further distinguish between caterpillars of the three
176 major Lepidoptera families presented in the study area: Tortricidae, Noctuidae and
177 Geometridae. The second group "others" include: 'spiders' (Aranea), 'imago' (belonging to
178 the orders Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera and Orthoptera),
179 'Chrysalides' and 'Miscellaneous' (heterogeneous group including plant tissues, fungus,

eggshell, snails and lichen). Size of preys was assessed using a scale bar attached above the entrance of the nest box as a reference. Within each taxonomic category, items of prey were classified to three ordinal categories of body size [1 = small (length <1.5 cm for caterpillars; <1.5 cm for imagos and abdomen diameter <0.2 cm for spiders); 2 = medium (length 1.5–2.5 cm, 1.5–2 cm and diameter 0.2–0.6 cm, respectively); 3 = large (length >2.5 cm for both caterpillars and imagos and diameter >0.6 cm for spiders)] to make individual prey volumes comparable among taxa (see García-Navas and Sanz, 2010). Shannon index H' was calculated for each nest.

2.4. Statistical analysis

Only first clutches were used. A set of General Linear Mixed Models (GLMM) were performed in all cases with year and patch size category as fixed factors and laying date as a covariate. As mentioned above, body condition of birds was estimated by adding the tarsus length as another covariate, as advised by Darlington and Smulders (2001) and García-Berthou (2001). In all models, nest ID nested in forest patch ID was included as the random term. Normal distribution was assumed in all models, with the exceptions of proportions (occupation rate, hatching success, fledgling success and proportions of the main prey). For these analyses, GLMMs with a binomial distribution and a binary response variable were employed. In the occupation rate model the numerator of the binary response variable was the number of occupied nest-boxes and the denominator was the total number of available nest-boxes in each forest patch. In hatching and fledgling success models, the numerator was the number of hatchlings and fledglings respectively, and the denominator was the clutch size and the number of hatchlings respectively. For proportions of the main

prey types, the numerator was the number of preys belonging to a specific prey type and the denominator was the total number of prey. Age of parents and probability to recruit next year were also analysed fitting the GLMMs with a binomial distribution. In age models the response variable was 0 for yearlings and 1 for adults; and in recruitment models the response variable was 0 for nestlings non-recruited and 1 for nestlings recruited. Nestling mass and nestling tarsus length were included as explanatory variables in the models of recruitment. Because in a fragmented landscape an increase of nest predation in small forest patches due to edge effects may also drive a worsening in the breeding success (Robinson et al., 1995; Chalfoun et al., 2002), we also tested the effect of the forest patch size on the predation rate by the ladder snake in both tit populations. The former analysis was also carried out fitting a GLMM with a binomial distribution, in which the dependent variable was 0 for non-predated nests and 1 for predated nests. When the interaction between the factor 'Year' and 'Patch size' was significant, the main effects of both factors on the response variable were not considered (even when $P< 005$), in a similar way as MacDonald et al. (2014). From the 329 blue tit nests used in this study, 28 females and 32 males were duplicated among years; and from the 161 great tit nests used, the number of duplicated adults was 11 females and 6 males. We performed the analysis with and without these duplicate adults and found no difference in the results. Thus, we decided to treat each adult as independent in the analyses, in the same way as Camfield and Martin (2013).

Assumptions of homogeneity, normality and independence were visually verified plotting the residuals against fixed values, doing a histogram of the residuals and plotting the residuals against each explanatory variable respectively (Zuur et al., 2009). All models were firstly constructed with all explanatory terms fitted including interactions, and final

models were selected following a backward procedure, by progressively eliminating non-significant terms starting with the interactions. Therefore, final models were those that explained the maximum variance with the least number of explanatory variables. All analyses were performed in R (R Core Team 2014) with the package lme4 (Bates et al., 2014). For non-parametric distributions Wald chi-square statistic (χ^2) is given. Mean ± SE (n) is given in the results.

3. Results

3.1. Occupation rate and breeding density

Nest-box occupation rate was higher in blue tits than in great tits [GLMM: Estimate ± SE= -0.98 ± 0.12, $\chi^2_{1, 70}$= 71.58, *P*< 0.001. Blue tits= 47.53 % ± 3.24 (41) and great tits= 38.39 % ± 4.19 (35)]. Regarding yearly variation, great tits increased their nest-box occupation rate in 2012, while years 2011 and 2013 did not differ (GLMM: $\chi^2_{2, 30}$= 36.75, *P*< 0.001. See Table 1). In contrast, nest-box occupation rate of blue tits did not change among years (GLMM: $\chi^2_{2, 36}$= 0.03, *P*= 0.99. See Table 2). In both species, the nest-box occupation rate was higher in small patches (Great tits, GLMM: Estimate ± SE= 1.75 ± 0.27, $\chi^2_{1, 30}$= 42.37, *P*< 0.001; large patches= 13.75 % ± 3.29 (9) and small patches= 46.92 % ± 4.43 (26). Blue tits, GLMM: Estimate ± SE= 0.71 ± 0.27, $\chi^2_{1, 38}$= 6.92, *P*= 0.008; large patches= 34.31 % ± 3.36 (9) and small patches= 51.25 % ± 3.80 (32). See Table 1 and 2 respectively).

Regarding the density of breeding pairs, there was not difference between species [GLMM: Estimate ± SE= 0.05 ± 0.18, $F_{1, 482}$= 0.08, *P*= 0.78. Blue tits= 5.40 % ± 0.14 (329)

and great tits= 5.52 % ± 0.21 (161)]; and both species increased their breeding density in 2012, whereas the breeding density between the years 2011 and 2013 did not differ (Great tits, GLMM: $F_{2, 153}$= 9.97, *P*< 0.001. Blue tits, GLMM: $F_{2, 322}$= 32.97, *P*< 0.001; Table 1 and 2 respectively). Breeding density of great tits was also positively affected by the laying date (GLMM: Estimate ± SE= 0.03 ± 0.01, $F_{1, 153}$= 6.87, *P*= 0.01). As regards the forest patch size effect, both tit species presented a higher breeding density in large forest patches than in small ones (Great tits, GLMM: Estimate ± SE= -3.43 ± 0.35, $F_{1, 153}$= 98.61, *P*< 0.001; large patches= 6.89 % ± 0.24 (99) and small patches= 3.34 % ± 0.14 (62). Blue tits, GLMM: Estimate ± SE= -3.30 ± 0.44, $F_{1, 322}$= 55.71, *P*< 0.001. Table 1 and 2 respectively).

257 **Table 1.** Summary of the occupation, density, predation, morphometric characteristics of adults and nestlings and reproductive
258 parameters in a population of great tits (*Parus major*) breeding in large and small oak forest patches in San Pablo de los Montes
259 (central Spain). Values given are Mean ± SE (n). Sample sizes vary accordingly to nest failures and missing adults.

Great tits						
	2011		2012		2013	
	Large patch	Small patch	Large patch	Small patch	Large patch	Small patch
Occupation rate (%)	5.42 ± 2.20 (3)	37.14 ± 6.80 (7)	23.75 ± 6.16 (3)	60.00 ± 8.94 (10)	12.08 ± 1.10 (3)	40.00 ± 3.33 (9)
Density (No. Pairs x Ha^{-1})	5.85 ± 0.88 (13)	3.23 ± 0.34 (13)	7.75 ± 0.29 (57)	3.52 ± 0.19 (31)	5.66 ± 0.31 (29)	3.11 ± 0.23 (18)
Nest predation (%)	0 (13)	0 (13)	42.11 ± 6.59 (57)	16.12 ± 6.72 (31)	17.24 ± 7.13 (29)	5.56 ± 5.56 (18)
Female age	-	-	0.41 ± 0.08 (32)	0.52 ± 0.12 (17)	0.77 ± 0.09 (22)	0.57 ± 0.14 (14)
Male age	-	-	0.69 ± 0.09 (29)	0.44 ± 0.13 (16)	0.89 ± 0.07 (19)	0.54 ± 0.14 (13)
Female mass (g)	-	-	16.18 ± 0.21 (32)	16.66 ± 0.21 (17)	16.94 ± 0.18 (22)	16.84 ± 0.20 (14)
Male mass (g)	-	-	17.12 ± 0.19 (29)	17.22 ± 0.25 (16)	17.77 ± 0.14 (19)	17.46 ± 0.22 (13)
Female tarsus length (mm)	-	-	19.12 ± 0.10 (32)	19.21 ± 0.09 (17)	19.29 ± 0.13 (22)	19.10 ± 0.13 (14)
Male tarsus length (mm)	-	-	19.89 ± 0.11 (29)	19.86 ± 0.15 (16)	20.01 ± 0.16 (19)	19.78 ± 0.11 (13)
Laying date	16.15 ± 2.87 (13)	13.62 ± 3.25 (13)	27.59 ± 2.00 (57)	23.87 ± 3.01 (31)	22.72 ± 1.32 (29)	21.72 ± 1.45 (18)
Clutch size	9.46 ± 0.44 (13)	9.62 ± 0.35 (13)	8.84 ± 0.26 (57)	8.19 ± 0.34 (31)	9.62 ± 0.35 (29)	9.11 ± 0.43 (18)
Hatching success (%)	78.07 ± 5.96 (13)	84.08 ± 7.42 (13)	65.82 ± 4.95 (32)	76.46 ± 6.26 (18)	66.12 ± 7.94 (23)	75.83 ± 6.76 (16)
Fledgling success (%)	91.88 ± 5.51 (13)	87.71 ± 8.28 (13)	86.67 ± 6.31 (30	86.58 ± 6.63 (17)	96.60 ± 2.29 (18)	77.71 ± 10.50 (15)
Nestling mass (g)	17.21 ± 0.27 (13)	16.87 ± 0.24 (13)	16.34 ± 0.19 (30)	16.02 ± 0.21 (18)	17.23 ± 0.18 (22)	16.96 ± 0.19 (12)
Nestling tarsus length (mm)	19.63 ± 0.12 (13)	19.44 ± 0.12 (13)	19.33 ± 0.09 (30)	19.19 ± 0.12 (18)	19.45 ± 0.07 (22)	19.10 ± 0.12 (12)
Recruitment (%)	-	-	4.83 ± 1.26 (290)	4.20 ± 1.84 (119)	0.88 ± 0.62 (226)	0 (122)

260 *3.2. Parents*

261 The body condition of blue and great tits decreased in 2012 (GLMM: Estimate ±
262 SE= 0.49 ± 0.20, $F_{1, 74}$= 6.12, P= 0.02 and GLMM: Estimate ± SE= 0.51 ± 0.21, $F_{1, 68}$=
263 5.97, P= 0.02 for great tit females and males respectively, and GLMM: $F_{2, 255}$= 4.37, P=
264 0.01 and GLMM: $F_{2, 211}$= 8.46, P< 0.001 for blue tit females and males respectively. See
265 Tables 1 and 2). In 2012, the proportion of yearlings to adults of female great tits increased
266 (GLMM: Estimate ± SE= 1.09 ± 0.49, $\chi^2_{1, 78}$= 5.09, P= 0.02. Table 1), the same as the
267 proportion of blue tit male yearlings (GLMM: $\chi^2_{1, 227}$= 8.21, P= 0.02. Table 2). Attending
268 the forest patch size effect, only males differed between patch size categories, although in a
269 different way in each species. The proportion of old great tit males was higher in large
270 patches (GLMM: Estimate ± SE= -1.19 ± 0.52, $\chi^2_{1, 69}$= 5.16, P= 0.02. Table 1), while blue
271 tit males had a better body condition in small patches (GLMM: Estimate ± SE= 0.29 ±
272 0.08, $F_{1, 211}$= 11.91, P< 0.001. Table 2).

273 **Table 2.** Summary of the occupation, density, predation, morphometric characteristics of adults and nestlings and reproductive
274 parameters in a population of blue tits (*Cyanistes caeruleus*) breeding in large and small oak forest patches in San Pablo de los Montes
275 (central Spain). Values given are Mean ± SE (n). Sample sizes vary accordingly to nest failures and missing adults.

Blue tits						
	2011		2012		2013	
	Large patch	Small patch	Large patch	Small patch	Large patch	Small patch
Occupation rate (%)	32.92 ± 3.97 (3)	56.67 ± 6.89 (12)	34.58 ± 9.02 (3)	52.50 ± 7.50 (8)	35.42 ± 6.05 (3)	45.00 ± 5.57 (12)
Density (No. Pairs x Ha^{-1})	5.52 ± 0.26 (79)	2.85 ± 0.21 (34)	7.40 ± 0.24 (83)	2.90 ± 0.21 (21)	5.87 ± 0.20 (85)	2.63 ± 0.22 (27)
Nest predation (%)	6.32 ± 2.75 (79)	2.94 ± 2.94 (34)	24.09 ± 0.05 (83)	19.05 ± 8.78 (21)	0.12 ± 3.52 (85)	14.81 ± 6.97 (27)
Female age	0.51 ± 0.06 (73)	0.61 ± 0.09 (31)	0.61 ± 0.07 (57)	0.60 ± 0.13 (15)	0.64 ± 0.05 (73)	0.57 ± 0.11 (23)
Male age	0.81 ± 0.05 (57)	0.70 ± 0.09 (27)	0.59 ± 0.07 (51)	0.83 ± 0.11 (12)	0.85 ± 0.04 (66)	0.85 ± 0.08 (20)
Female mass (g)	9.66 ± 0.06 (73)	9.51 ± 0.10 (31)	9.22 ± 0.13 (57)	9.62 ± 0.10 (15)	9.69 ± 0.06 (73)	9.55 ± 0.09 (23)
Male mass (g)	9.80 ± 0.06 (57)	9.83 ± 0.09 (27)	9.18 ± 0.11 (51)	9.82 ± 0.10 (12)	9.71 ± 0.05 (66)	10.15 ± 0.22 (20)
Female tarsus length (mm)	15.81 ± 0.06 (73)	15.66 ± 0.11 (31)	15.79 ± 0.06 (57)	16.21 ± 0.16 (15)	15.86 ± 0.05 (73)	16.00 ± 0.11 (23)
Male tarsus length (mm)	16.29 ± 0.07 (57)	16.23 ± 0.10 (27)	16.30 ± 0.07 (51)	16.34 ± 0.14 (12)	16.32 ± 0.06 (66)	16.30 ± 0.09 (20)
Laying date	18.63 ± 1.36 (79)	14.59 ± 2.11 (34)	24.82 ± 1.24 (83)	26.95 ± 2.97 (21)	29.13 ± 1.5 (85)	28.44 ± 1.89 (27)
Clutch size	8.14 ± 0.24 (79)	9.03 ± 0.32 (34)	8.63 ± 0.24 (83)	7.43 ± 0.51 (21)	8.19 ± 0.19 (85)	8.89 ± 0.34 (27)
Hatching success (%)	82.23 ± 2.34 (73)	74.97 ± 5.05 (33)	69.79 ± 3.84 (62)	75.39 ± 6.30 (13)	79.07 ± 3.35 (72)	85.83 ± 3.47 (22)
Fledgling success (%)	92.42 ± 3.01 (72)	96.67 ± 3.33 (30)	84.62 ± 4.19 (55)	75.38 ± 10.38 (13)	89.61 ± 2.94 (68)	83.33 ± 7.60 (22)
Nestling mass (g)	10.10 ± 0.07 (67)	9.85 ± 0.08 (29)	9.34 ± 0.13 (53)	9.36 ± 0.28 (11)	10.24 ± 0.07 (69)	10.03 ± 0.16 (21)
Nestling tarsus length (mm)	15.90 ± 0.06 (67)	15.82 ± 0.07 (29)	15.67 ± 0.05 (53)	15.75 ± 0.21 (11)	15.88 ± 0.05 (69)	16.03 ± 0.12 (21)
Recruitment (%)	-	-	10.18 ± 1.27 (570)	2.61 ± 1.05 (230)	1.97 ± 0.69 (406)	1.41 ± 1.41 (71)

276 *3.3. Breeding performance*

277 The greatest differences in the breeding performance of tits were given among years
278 (Table 3). Blue tit laying date was delayed year after year (Table 2. Tukey HSD test< 0.05),
279 and their hatching success, nestling condition, nestling size and recruitment decreased in
280 2012 (Table 2 and 3. Tukey HSD test< 0.05); contrary to nest predation, which increased in
281 2012 (Table 2 and 3). Great tits showed a similar phenology than blue tits, and their laying
282 date was also delayed in 2012 and 2013, although there were not differences between these
283 latter years (Table 1 and 3. Tukey HSD test> 0.05). The clutch size in this species did not
284 differ among years (Table 3). Rest of the reproductive variables varied among years in a
285 similar way as blue tits, i.e. decreasing in 2012 (see Table 1. Tukey HSD test< 0.05),
286 except for the hatching success and nest predation (Table 3).

287 In both species, the main difference found between forest patch size categories was
288 at nestling stage. The tarsi of great tit nestlings in large patches was longer than the tarsi of
289 conspecifics in small patches all years (large patches: 19.43 ± 0.06 (65), small patches:
290 19.23 ± 0.07 (42). Tables 1 and 3), while the body condition of blue tit nestlings in large
291 patches was better than conspecifics in small patches (large patches: 9.94 g ± 0.05 (189),
292 small patches: 9.72 g ± 0.08 (61). Tables 2 and 3). The nestling body condition in both
293 species was also positively affected by their tarsus length (Table 3). Regarding recruitment,
294 the probability of a blue tit yearling that was born in the study area to breed the next year,
295 was higher for those that were born in large patches; whereas in great tits, it was positively
296 related to their body mass (Table 3). Almost none other trait of breeding performance
297 differed between patch size categories, although there were some significant interactions

298 between year and patch size category in blue tits (Table3). Concretely, the clutch size and
299 fledgling success differed in 2012, being smaller in small patches (Table 2), in rest of years
300 these variables did not differ between patch size categories.

Table 3. Results of the GLMMs showing the effects of year, patch size and laying date on the breeding performance of blue (*Cyanistes caeruleus*) and great tits (*Parus major*) in Montes de Toledo, central Spain. The ID nest localized in ID forest patch is included in all models as the random effect. *F* statistic is used for Laying date, Clutch size and Nestling condition and size; while χ^2 statistic is used for Hatching and Fledgling success, Predation rate and Recruitment. Statistics of non-significant terms are shown in Table S1.

Blue tit					Great tit				
Parameter	Effect	d.f.	test	*P*	Parameter	Effect	d.f.	test	*P*
Laying date	Year	320	32.2	<0.001	**Laying date**	Year	150	8.1	<0.001
Rejected effects: Patch size and Year * Patch size.					Rejected effects: Patch size and Year * Patch size.				
Clutch size	Laying date	316	164.5	<0.001	**Clutch size**	Laying date	149	13.3	<0.001
	Year*Patch size	316	3.3	0.02					
Rejected effects: Patch size.					Rejected effects: Year, Patch size and Year * Patch size.				
Hatch. success	Year	296	6.9	0.03	**Hatch. success**				
Rejected effects: Patch size, Laying date and Year * Patch size.					Rejected effects: All.				
Fledg. success	Laying date	251	35.2	<0.001	**Fledg. success**	Year	100	11.8	0.003
	Year*Patch size	251	13.7	0.003					
Rejected effects: Patch size.					Rejected effects: Patch size, Laying date and Year * Patch size.				
Nest predation	Year	320	15.77	<0.001	**Nest predation**				
Rejected effects: Patch size, Laying date and Year * Patch size.					Rejected effects: All				
Nest. condition	Year	224	26.4	<0.001	**Nest. condition**	Year	94	11.5	<0.001
	Patch size	224	5.5	0.02		Tarsus length	95	36.1	<0.001
	Laying date	224	5.5	<0.001					
	Tarsus length	224	28.6	<0.001					
Rejected effects: Year * Patch size.					Rejected effects: Patch size, Laying date and Year * Patch size.				
Nestling size	Year	225	6.9	0.001	**Nestling size**	Year	95	3.5	0.03
	Laying date	225	5.3	0.02		Patch size	95	4.9	0.03
Rejected effects: Patch size and Year * Patch size.					Rejected effects: Laying date and Year * Patch size.				
Recruitment	Year	1274	20.9	<0.001	**Recruitment**	Year	787	6.1	0.01
	Patch size	1274	6.3	0.01		Nestling mass	787	5.9	0.02
Rejected effects: Nestling mass, Tarsus length, Laying date and Year * Patch size.					Rejected effects: Patch size, Tarsus length, Laying date and Year * Patch size.				

307 *3.4. Nestling diet*

308 Table S2 resumes the nestling diet of each species in each forest patch size category
309 and year. Regarding the nestling diet of each species, the greatest differences were given
310 among years. The proportion of caterpillars in blue tit nestling diet increased in 2012 and
311 2013 in relation to 2011 (Tukey HSD test< 0.05, Table 4), but these increases were
312 sustained by different caterpillar families in each year. In 2012 the increase in the
313 proportion of caterpillars delivered by blue tits was above all due to an increase in the
314 intake of noctuids, while the proportion of tortricids this year decreased (Tukey HSD test<
315 0.05). This increase in the consumption of noctuids in 2012 was probably the cause of the
316 increase in the prey size this year (Tukey HSD test <0.05). In 2013 the proportion of
317 noctuids diminished, but the proportion of tortricids increased with respect to the former
318 years (Tukey HSD test <0.05, Table 4), resulting in the highest proportion of caterpillar in
319 nestling diet this year. The proportion of spiders decreased in 2013 (Tukey HSD test
320 <0.05). In this species, the forest patch size did not affect the nestling diet (Table 4).
321 However, the proportions of total caterpillars, noctuids, tortricids and prey size were
322 negatively affected by the date, while proportion of spiders increased with the date; both in
323 a linear way (Table 4). Feeding rate was only positively affected by the brood size. Finally,
324 the proportion of noctuids was negatively affected by brood size, whereas the proportion of
325 tortricids was positively affected (Table 4). Diet diversity (H') in this species did not vary
326 between patch sizes or years, but was positively affected by both laying date and brood size
327 (GLMM: Estimate ± SE: 0.009 ± 0.03, $F_{1, 177}$= 9.12, P= 0.003 and GLMM: Estimate ± SE:
328 0.04 ± 0.01, $F_{1, 177}$= 6.26, P= 0.01).

329 **Table 4.** Results of the GLMMs analyzing the effects of the year, patch size, laying date and brood size on blue tit nestlings diet
330 (*Cyanistes caeruleus*) in Montes de Toledo, central Spain. The ID nest nested in ID forest patch is included in all models as the random
331 term. Wald chi-square (χ^2) statistic is given with non-parametric distributions. Significant results are highlighted in bold.
332

Response variable	Explanatory term	Estimate ± SE	test	*P*	Response variable	Explanatory term	Estimate ± SE	test	*P*
Feeding rate	Intercept	8.44 ± 3.04			Tortricidae	Intercept	-2.00 ± 0.32		
	Year		$F_{2, 175}$= 1.84	0.16		Year		$\chi^2_{2, 176}$= 37.57	**<0.001**
	Patch size	-4.02 ± 2.47	$F_{1, 176}$= 2.64	0.13		Patch size	0.08 ± 0.20	$\chi^2_{1, 175}$= 0.17	0.68
	Laying date	-0.08 ± 0.09	$F_{1, 174}$= 0.74	0.40		laying date	-0.01 ± 0.005	$\chi^2_{1, 176}$= 5.13	**0.02**
	Brood size	2.50 ± 0.39	$F_{1, 177}$= 40.31	**<0.001**		Brood size	0.08 ± 0.03	$\chi^2_{1, 176}$= 5.52	**0.02**
	Year*Patch size		$F_{2, 172}$= 0.09	0.92		Year*Patch size		$\chi^2_{2, 173}$= 4.24	0.12
Caterpillars	Intercept	1.48 ± 0.13			Aranea	Intercept	-1.93 ± 0.10		
	Year		$\chi^2_{2, 177}$= 11.32	**0.003**		Year		$\chi^2_{2, 177}$= 24.33	**<0.001**
	Patch size	-0.11 ± 0.16	$\chi^2_{1, 176}$= 0.50	0.48		Patch size	-0.07 ± 0.10	$\chi^2_{1, 175}$= 0.40	0.52
	laying date	-0.03 ± 0.004	$\chi^2_{1, 177}$= 38.87	**<0.001**		laying date	0.009 ± 0.004	$\chi^2_{1, 177}$= 5.21	**0.02**
	Brood size	-0.007 ± 0.03	$\chi^2_{1, 175}$= 0.08	0.78		Brood size	-0.03 ± 0.004	$\chi^2_{1, 176}$= 1.67	0.20
	Year*Patch size		$\chi^2_{2, 173}$= 3.02	0.22		Year*Patch size		$\chi^2_{2, 173}$= 4.22	0.12
Noctuidae	Intercept	0.51 ± 0.23			Prey size	Intercept	1.99 ± 0.08		
	Year		$\chi^2_{2, 176}$= 16.38	**<0.001**		Year		$F_{2, 176}$= 18.30	**<0.001**
	Patch size	-0.09 ± 0.17	$\chi^2_{1, 175}$= 0.32	0.57		Patch size	-0.008 ± 0.08	$F_{1, 175}$= 0.01	0.92
	laying date	-0.02 ± 0.004	$\chi^2_{1, 176}$= 12.48	**<0.001**		laying date	-0.007 ± 0.003	$F_{1, 176}$= 4.52	**0.04**
	Brood size	-0.05 ± 0.02	$\chi^2_{1, 176}$= 4.35	**0.03**		Brood size	-0.002 ± 0.02	$F_{1, 172}$= 0.02	0.89
	Year*Patch size		$\chi^2_{2, 173}$= 0.36	0.84		Year*Patch size		$F_{2, 173}$= 2.56	0.08

Attending great tit nestling diet, they showed a similar yearly pattern than blue tits. The proportion of caterpillars increased in 2012 and 2013, although it did not differ between the latter years (Tukey HSD test> 0.05); in the same way as the proportion of noctuids (Table 5). The proportion of spiders also diminished in 2013 in this species (Tukey HSD test< 0.05). Opposite to blue tits, proportion of tortricids and prey size were not affected by any explanatory variable (Table 5). In this species, the forest patch size did affect the nestling diet. Concretely, the proportions of caterpillars and noctuids were higher in large patches (Table 5 and S2). These two prey types were also negatively affected by the date. As in blue tits, feeding rate was positively affected by the brood size, but no prey type was (Table 5). Diet diversity (H') in this species was only affected by the patch size, being higher in large patches (GLMM: Estimate ± SE: 0.32 ± 0.15, $F_{1, 56}$= 4.37, P= 0.04).

Table 5. Results of the GLMMs analyzing the effects of the year, patch size, laying date and brood size on great tit nestlings diet (*Parus major*) in Montes de Toledo, central Spain. The ID nest nested in ID forest patch is included in all models as the random term. Wald chi-square (χ^2) statistic is given with non-parametric distributions. Significant results are highlighted in bold.

Response variable	Explanatory term	Estimate ± SE	test	*P*	Response variable	Explanatory term	Estimate ± SE	test	*P*
Feeding rate	Intercept	8.40 ± 3.68			Tortricidae	Intercept	-2.45 ± 0.19		
	Year		$F_{2, 49}$= 0.09	0.91		Year		$\chi^2_{2, 53}$= 0.97	0.61
	Patch size	-0.83 ± 5.78	$F_{1, 49}$= 0.03	0.87		Patch size	-0.32 ± 0.33	$\chi^2_{1, 55}$= 0.96	0.32
	laying date	-0.09 ± 0.09	$F_{1, 54}$= 1.07	0.30		laying date	-0.02 ± 0.01	$\chi^2_{1, 54}$= 1.63	0.20
	Brood size	1.02 ± 0.45	$F_{1, 55}$= 5.15	**0.03**		Brood size	-0.01 ± 0.07	$\chi^2_{1, 52}$= 0.03	0.87
	Year*Patch size		$F_{5, 49}$= 2.71	0.06		Year*Patch size		$\chi^2_{2, 50}$= 2.00	0.37
Caterpillars	Intercept	2.28 ± 0.52			Aranea	Intercept	-2.34 ± 0.34		
	Year		$\chi^2_{2, 53}$= 20.80	**<0.001**		Year		$\chi^2_{2, 55}$= 13.10	**0.001**
	Patch size	-1.01 ± 0.41	$\chi^2_{1, 53}$= 5.93	**0.01**		Patch size	0.14 ± 0.43	$\chi^2_{1, 53}$= 0.10	0.75
	laying date	-0.05 ± 0.001	$\chi^2_{1, 53}$= 10.17	**0.001**		laying date	0.001 ± 0.02	$\chi^2_{1, 52}$= 0.005	0.95
	Brood size	-0.01 ± 0.08	$\chi^2_{1, 52}$= 0.02	0.89		Brood size	-0.03 ± 0.10	$\chi^2_{1, 54}$= 0.13	0.72
	Year*Patch size		$\chi^2_{2, 50}$= 0.95	0.62		Year*Patch size		$\chi^2_{2, 50}$= 0.51	0.77
Noctuidae	Intercept	0.93 ± 0.41			Prey size	Intercept	2.15 ± 0.08		
	Year		$\chi^2_{2, 51}$= 21.93	**<0.001**		Year		$F_{2, 54}$= 1.65	0.21
	Patch size	-0.60 ± 0.31	$\chi^2_{1, 51}$= 4.34	**0.03**		Patch size	0.05 ± 0.15	$F_{1, 51}$= 0.11	0.75
	laying date	-0.04 ± 0.01	$\chi^2_{1, 51}$= 8.82	**0.002**		laying date	-0.007 ± 0.01	$F_{1, 53}$= 1.71	0.20
	Brood size	0.02 ± 0.06	$\chi^2_{1, 50}$= 0.09	0.76		Brood size	-0.02 ± 0.03	$F_{1, 52}$= 0.83	0.37
	Year*Patch size		$\chi^2_{2, 48}$= 2.17	0.34		Year*Patch size		$F_{2, 49}$= 0.85	0.44

353 **4. Discussion**

354 The nest-box occupation rate was higher in small forest patches for both species in
355 all years, probably because the lower availability of nest-boxes in such forest patches
356 limited the nest choice of tits (Barrientos et al., 2015). However, contrary to nest-box
357 occupation rate, the density of tit breeding pairs around each territory was higher in large
358 forest patches. This forest patch size effect on the breeding density was possibly due to the
359 greater availability of nest-boxes in the large forest patches. Breeding density is an
360 important trait that negatively influences the breeding performance and recruitment of birds
361 because of the competition over resources (Both, 1988; Both et al., 1999). However, the
362 nestling growth was better and the blue tit recruitment was higher in large patches, despite
363 the higher breeding density in those patches; which reinforces the idea that large forest
364 patches offer better conditions for breeding tits than small patches .

365 As we said before, patch size affected nestling growth in both species (Table 3).
366 Great tit nestlings in large patches were bigger than those from small patches, which
367 suggest that nestling growing conditions were better in large patches. Worse feeding
368 conditions in small patches may be behind the former result, as food is the main limiting
369 factor of nestling growth (Van Noordwijk et al., 1988). In fact, the analysis of great tit
370 nestling diet revealed key differences between patch size categories (Table 5). Great tits
371 delivered more caterpillars to theirs broods in large patches, in particular noctuids (Table
372 S2), which are the preferred prey of this species in the study area (García-Navas et al.,
373 2013). The possibility to feed with a higher proportion of their preferred prey in large
374 patches may not go unnoticed for great tits, and males may compete to settle there, as the

375 age pattern suggests. This difference in the average age of great tits between large and
376 small patches has been also shown in other studies with this species (Moller, 1991;
377 Riddington and Gosler, 1995) and other species (Burke and Nol, 1998); and is related to the
378 acquisition of a territory (Riddington and Gosler, 1995). In this species, the patch size did
379 not affect their recruitment; although it was positively affected by the nestling mass; as
380 other previous studies have shown (Tinbergen and Boerlijst, 1990; Verhulst et al., 1997).
381 Nonetheless, from all great tit fledglings that achieved to breed in the next year, 82% were
382 born in large patches (data not shown for brevity); and the 78% of them bred again in large
383 patches, versus the 50% of the nestlings that were born in small patches.

384 Blue tit nestlings did not differ in body size between patch size categories (Table 3);
385 which suggests that blue tit nestlings did not have the limitations in their development that
386 the great tit nestlings seem to suffer in small patches. The reason of this dissimilarity in the
387 results could rely in the different feeding habits of both species. Blue and great tits,
388 although they share a similar trophic ecology predating above all on Lepidoptera
389 caterpillars (Perrins, 1991), differ in the global amount of caterpillars in their diet and the
390 composition of them. Great tits are more specialists on caterpillars, being highly selective
391 for larger ones (Naef-Daenzer et al., 2001); which in our study area are chiefly noctuids.
392 Blue tits additionally, feed abundantly on tortricids and also incorporate a great amount of
393 spiders in their diet (García-Navas et al., 2013). The particular feeding behaviour of each
394 species was also highlighted when an increase in the parental effort was given. Both species
395 increased their feeding rate with large broods, but in a different way. Blue tits faced this
396 burden on parental effort through a change in the composition of their diet. This is partly
397 shown with the reduction in the proportion of caterpillar as broods become larger and also

398 with the increase in diet diversity (Table 4). An example of this switch in blue tit diet
399 according to the degree of parental effort, is what happens with the two most abundant
400 caterpillar families in our study area, noctuids and tortricids. The first ones, despite they are
401 a high quality prey, are scarce and more difficult to find. In contrast, tortricids are smaller
402 but their higher abundance, gregarious behaviour and leaf-roller habits make them easy to
403 find (Naef-Daenzer and Keller, 1999; García-Navas et al., 2013). With small broods, blue
404 tits feed their nestlings with a high proportion of noctuids but, as the broods become larger,
405 they start incorporating a higher proportion of tortricids at the expense of noctuids. This
406 change in the composition of the diet allows them to increase their feeding rate (Table 4).
407 This switch in blue tit diet accordingly to the degree of parental effort was experimentally
408 demonstrated by García-Navas and Sanz (2010). Great tits with larger broods did feed more
409 frequently but they did not change their nestling's diet composition (Table 5).

410 This wider trophic niche of blue tits (Matthysen et al., 2011), may allow them to
411 face more efficiently the food limitation conditions in small forest patches, and to better
412 satisfy the energetic demands of their broods in such patches. Indeed, their diet diversity
413 did not change between patch size categories; which means that they in general find their
414 food requisites in both patch size categories. This was not the case of great tits, which
415 increased their diet diversity in small patches, probably because they are not able to achieve
416 their preferred diet in those patches and are forced to shift to secondary low-quality preys.
417 Although the elementary feeding requisites of blue tits may be satisfied in small patches,
418 this does not mean that little differences in composition, even at species level (García-
419 Navas et al., 2013 and references there-in), influence the body condition of their nestlings
420 due to differences in food quality, as food is the main limiting factor in nestling body

condition (Naef-Daenzer and Keller, 1999; Kaliński et al., 2014). In fact, for blue tit nestlings was better to be born in large patches, because the probability to breed next year was higher in those patches (Table 3). In the same way as great tits, the 81% of the blue tit yearlings that achieved to breed were born in large patches, and the 97% of them did it in large patches. Surprisingly, blue tit males were heavier in small patches; which a priori goes against expectation. However, Riddington and Gosler (1995) found a similar result with great tit males breeding in good and poor habitats. The former authors discussed that in poor habitats, due to the scarcity of food, birds increase their fat reserves to face this uncertainty (McNamara and Houston, 1990; Higginson et al., 2012). This could be happening in our study area, although we could not confirm this, as we did not measured the fat score levels (Gosler, 1997). The forest patch size effect on nestling characteristics found in this study contrasts with the results obtained by Nour et al., (1998), where they did not find differences in the breeding success, diet or caterpillar abundances among a gradient of forest patch size categories. In our study area, although both patch size categories present a similar habitat structure, the small patches support a greater influx of people and the passage of cattle; which could have contributed for the worse breeding performance of tits in those forest patches due to annoyances.

Besides food supply, nest predation has been seen an important feature driving the worse breeding success of forest birds in small forest patches (Robinson et al., 1995; Chalfoun et al., 2002; Batáry et al., 2014). Nonetheless in this study, the forest patch size did not affect the predation rate of nests, probably because we protected the nest-boxes against most predator species; leading the ladder snake as the main predator in our study area. The snake was present in all forest patches, making the predation rate homogeneous in

444 the whole study area. The increase of the predation rate in 2012 could be related with the
445 increase of the breeding density this year, favouring an increase in the encounter rate of the
446 snakes with occupied nest-boxes.

447 Other feature that strongly marked this study was the yearly variation, probably
448 because of the different environmental conditions in each year; which had a large influence
449 on the abundance of caterpillars as temperature is the primary factor influencing their
450 phenology (Visser and Holleman, 2001). In year 2012, the budding of the oaks was
451 extremely delayed (some patches did not bud until mid-May, J. Bueno-Enciso pers. obs.).
452 This probably caused caterpillars hatched before this date to starve, as they only can
453 survive a few days without food (Durant et al., 2007). As a consequence, the abundance of
454 caterpillars this year likely decreased in comparison with the others; which probably
455 accounted for the decrease in the body condition and breeding performance of birds in
456 2012, due to the 'reproductive stress' hypothesis (Nagy et al., 2007; Neto and Gosler,
457 2010). This variation in the breeding performance among years is well documented in bird
458 population studies (Perrins, 1965, Lack, 1966). Tits also delayed their laying date in each
459 year, probably in an attempt to synchronize the period of maximum food demand of their
460 chicks with the peak of food (Van Noordwijk et al., 1995), a feature that enhances their
461 reproductive success (Visser et al., 2006; Cresswell and McCleery, 2003; Matthysen et al.,
462 2011). Blue tits, but not great tits, had a smaller clutch size and a worse breeding success in
463 small patches in 2012. This result may suggest that for some species, the effects of habitat
464 fragmentation only arise in certain years under particular conditions, such as a food
465 shortage; as other authors have pointed out (Riddington and Gosler, 1995; Nour et al.,
466 1998). In 2012, the proportion of yearlings to adults of blue tit males and great tit females

increased. This increase in the proportion of yearlings in 2012 was probably due to the effect of increasing the number of nest sites the former year, joined with the good environmental conditions prevailing in 2011; which allowed a higher recruitment rate in 2012 (Newton, 1994; Robles et al., 2012). Blue tit nestling diet varied among years probably in consonance with the prey availability in each year, because of their more flexible feeding behaviour (Matthysen et al., 2011). This was not the case of great tits, which actively selected noctuids, the consumption of which increased each year (Table 3). Consumption of spiders decreased in 2013 in both species, probably due to a sudden decline of this type of prey in the forest this year (Tables 4 and 5).

4.1. Conclusions

This study suggests that food supply in small forest patches could be hampering the growing conditions of tits in such forest patches, and consequently, their recruitment rate. However, the observational nature of this study does not allow firm conclusions to be drawn, and experiments of cross-fostering between large and small forest patches would be necessary to confirm the factors involved in the reduced breeding performance of tits in small forest patches.

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References

- Amos, J.N., Balasubramaniam, S., Grootendorst, L., Harrison, K.A., Lill, A., Mac Nally, R., Pavlova, A., Radford, J.Q., Takeuchi, N., Thompson, J.R., Sunnucks, P., 2013. Little evidence that condition, stress indicators, sex ratio or homocygosity are related to landscape or habitat attributes in declining woodland birds J. Avian Biol. 44, 045–054. doi: 10.1111/j.1600-048X.2012.05746.x
- Atiénzar, F., Álvarez, E., Barba, E., 2012. Carbonero común – *Parus major*. En: Enciclopedia Virtual de los Vertebrados Españoles. Salvador, A., Morales, M. B. (Eds.). Museo Nacional de Ciencias Naturales, Madrid. http://www.vertebradosibericos.org

- Barrientos, R., Bueno-Enciso, J., Serrano-Davies, E., Sanz, J.J., 2015. Facultative interspecific brood parasitism in tits: a last resort to coping with nest-hole shortage. Behav. Ecol. Sociobio 69, 1603–1615. doi: 10.1007/s00265

- Batáry, P., Fronczek, S., Normann, C., Scherber, C., Tscharntke, T., 2014. How do edge effect and tree species diversity change bird diversity and avian nest survival in Germany's largest deciduous forest?. Forest Ecol. Manag. 319, 44–50. doi:10.1016/j.foreco.2014.02.004

- Bates, D., Maechler, M., Bolker, B.M., Walker, S., 2014. lme4: Linear mixed-effects models using Eigen and S4. J Stat Softw. URL: http://arxiv.org/abs/1406.5823.

- Blondel, J., Aronson, J., 1999. Biology and wildlife of the Mediterranean region. Oxford (UK): Oxford University Press.

- Both, C., 1998. Density dependence of clutch size: habitat heterogeneity or individual plasticity? J. Anim. Ecol. 67, 659–666. doi: 10.1046/j.1365-2656.1998.00227.x

- Both, C., Visser, M.E., Verboven, N., 1999. Density-dependent recruitment rates in great tits: the importance of being heavier. Proc. R. Soc. Lond. Ser. B Biol. Sci. 266, 465–469. doi: 10.1098/rspb.1999.0660

- Boulinier, T., Nichols, J.D., Hines, J.E., Sauer, J.R., Flather, C.H., Pollock, K.H., 2001. Forest fragmentation and bird community dynamics: inference at regional scales. Ecology 82, 1159–1169. Doi:

- Bregman, T.P., Sekercioglu, C.H., Tobias, J.A., 2014. Global patterns and predictors of bird species responses to forest fragmentation: Implications for

532 ecosystem function and conservation. Biol. Conserv. 169, 372–383
533 doi:10.1016/j.biocon.2013.11.024
534 - Bruun, M., Smith, H.G., 2003. Landscape composition affects habitat use and
535 foraging flight distances in breeding European starlings. Biol. Conserv. 114, 179–
536 187. doi:10.1016/S0006-3207(03)00021-1
537 - Burke, D.M., Nol, E., 1998. Influence of food abundance, nest-site habitat, and
538 forest fragmentation on breeding Ovenbirds. The Auk 115, 96–104. doi:
539 10.2307/4089115
540 - Camfield, A.F., Martin, K., 2009. The influence of ambient temperature on horned
541 lark incubation behaviour in an alpine environment. Behaviour 146, 1615-1633. doi:
542 10.1163/156853909X463335
543 - Chalfoun, A.D., Thompson, F.R., Ratnaswamy, M.J., 2002. Nest predators and
544 fragmentation: a review and meta-analysis. Conserv. Biol. 16, 306–18. doi:
545 10.1046/j.1523-1739.2002.00308.x
546 - Cramp, S., Perrins, C.M., 1993. Handbook of the birds of Europe, the Middle East
547 and North Africa: The Birds of the Western Palearctic. Oxford University Press,
548 Oxford.
549 - Cresswell, W., McCleery, R.H., 2003. How great tits maintain synchronization of
550 their hatch date with food supply in response to long-term variability in
551 temperature. J. Anim. Ecol. 72, 356–366. doi: 10.1046/j.1365-2656.2003.00701.x
552 - Darlington, R.B., Smulders, T.V., 2001. Problems with residual analysis. Anim.
553 Behav. 62, 599–602. doi: 10.1006/anbe.2001.1806

554 - Debinski, D.M., Holt, R.D., 2000. A survey and overview of habitat fragmentation
555 experiments. Conserv. Biol. 14, 342–355. doi: 10.1046/j.1523-1739.2000.98081.x

556 - Desrochers, A., Hannon, S.J., 1997. Gap crossing decisions by forest songbirds
557 during the post-fledging period. Conserv. Biol. 11, 1204–1210. doi: 10.1046/j.1523-
558 1739.1997.96187.x

559 - Didham, R.K., Ghazoul, J., Stork, N.E., Davis, A.J., 1996. Insects in fragmented
560 forests: a functional approach. Trends Ecol. Evol. 11, 255–260. doi: 10.1016/0169-
561 5347(96)20047-3

562 - Durant, J.M., Hjermann, D.Ø., Ottersen, G., Stenseth, N.C., 2007. Climate and the
563 match or mismatch between predator requirements and resource availability. Clim.
564 Res. 33, 271–283. doi:10.3354/cr033271

565 - Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol.
566 Evol. Syst. 34, 487–515. doi: 10.1146/annurev.ecolsys.34.011802.132419

567 - Frey-Roos, F., Brodmann, F., Reyer, H.U., 1995. Relationship between food
568 resources, foraging patterns and reproductive success in the water pipit *Anthus sp.*
569 *spinoletta*. Behav. Ecol. 6, 287–295. doi: 10.1093/beheco/6.3.287

570 - García-Berthou, E., 2001. On the misuse of residuals in ecology: testing regression
571 residuals vs. the analysis of covariance. J. Anim. Ecol. 70, 708–711. doi:
572 10.1046/j.1365-2656.2001.00524.x

- García-Navas, V., Sanz, J.J., 2010. Flexibility in the Foraging Behavior of Blue Tits in Response to Short-Term Manipulations of Brood Size. Ethology 116, 744–755. doi: 10.1111/j.1439-0310.2010.01788.x

- García-Navas, V., Sanz, J.J., 2011. The importance of a main dish: nestling diet and foraging behaviour in Mediterranean blue tits in relation to prey phenology. Oecologia 165, 639–49. doi: 10.1007/s00442-010-1858-z

- García-Navas, V., Sanz, J.J., 2012. Environmental and within-nest factors influencing nestling-feeding patterns of Mediterranean blue tits (*Cyanistes caeruleus*). The Condor 114, 612–621. doi.org/10.1525/cond.2012.110120

- García-Navas, V., Ferrer, E.S., Sanz, J.J., 2013. Prey choice, provisioning behaviour, and effects of early nutrition on nestling phenotype of titmice[1]. Ecoscience 20, 9–18. doi: 10.2980/20-1–3545

- Gosler, A.G., 1997. Environmental and social determinats of winter fat storage in the Great tit *Parus major*. J. Anim. Ecol. 65, 1–17. doi: 10.2307/5695

- Helzer, C.J., Jelinski, D.E., 1999. The relative importance of patch area and perimeter-area ratio to grassland breeding birds. Ecol. Appl. 9, 1448–1458. doi: 10.1890/1051-0761(1999)009[1448:TRIOPA]2.0.CO;2

- Higginson, A.D., McNamara, J.M., Houston, A.I., 2012. The Starvation-Predation Trade-Off Predicts Trends in Body Size, Muscularity, and Adiposity between and within Taxa. Amer. Nat. 179, 338–350. doi: 10.1086/664457

- Hinam, H.L., Clair, C.C.S., 2008. High levels of habitat loss and fragmentation limit reproductive success by reducing home range size and provisioning rates of

595 Northern saw-whet owls. Biol. Conserv. 141, 524–535. doi:
596 10.1016/j.biocon.2007.11.011

597 - Hinsley, S.A., 2000. The costs of multiple patch use by birds. Landsc. Ecol. 15,
598 765–775. doi: 10.1023/A:1008149403852
599 - Hinsley, S.A., Rothery, P., Bellamy, P.E., 1999. Influence of woodland area on
600 breeding success in Great Tits (*Parus major*) and Blue Tits (*Parus caeruleus*). J.
601 Avian Biol. 30, 271–281. doi: 10.2307/3677353

602 - Hinsley, S.A., Hill, R.A., Bellamy, P., Broughton, R.K., Harrison, N.M.,
603 Mackenzie, J.A., Speakman, J.R., Ferns, P.R., 2009. Do Highly Modified
604 Landscapes Favour Generalists at the Expense of Specialists? An Example using
605 Woodland Birds. Landsc. Res. 34, 509–536. doi: 10.1080/01426390903177276

606 - Kaliński, A., Bańbura, M., Gladąlski, M., Markowski, M., Skwarska, J.,
607 Wawrzyniak, J., Zieliński, P., Cyżewska, I., Bańbura, J., 2014. Landscape patterns
608 of variation in blood glucose concentration of nestling blue tits (*Cyanistes*
609 *caeruleus*). Landscape Ecol. 29, 1521–1530. doi: 10.1007/s10980-014-0071-6
610 - Kuitunen, M., Makinen, M., 1993. An experiment on nest-site choice of the
611 common treecreeper in fragmented boreal forest. Ornis Fennica 70, 163–167
612 - Lack, D., 1966. Population studies of birds. Clarendon, Oxford, England.
613 - Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London
614 - Lampila, P., Mönkönen, M., Desrochers, A. 2005. Demographic responses by birds
615 to forest fragmentation. Conserv. Biol. 19, 1537–1546. doi: 10.1111/j.1523-
616 1739.2005.00201.x

- Laurance, W.F., 2010. Habitat destruction: death by a thousand cuts. In: Conservation Biology for all, Chapter 4. Ed. Sodhi NS and Ehrlich PR, Pp. 73–87. Oxford University press. Oxford, UK.
- Laurance, W.F., Lovejoy, T.E., Vasconcelos, H.L., Bruna, E.M., Didham, R.K., Stouffer, P.C., Gascon, C., Bierregaard, R.O., Laurance, S.G., Sampaio, E., 2002. Ecosystem Decay of Amazonian Forest Fragments: a 22-Year Investigation. Conserv. Biol. 16, 605–618. doi: 10.1046/j.1523-1739.2002.01025.x
- Le Tortorec, E., Huelle, S., Suorsa, P., Hakkerainen, H., 2012. Parental and genetic factors rather than nesting forest patch size affect physiological traits of offspring in an area-sensitive passerine: an experimental study. Ibis 154, 345–353. doi: 10.1111/j.1474-919X.2012.01219.x
- Loman, J. 2003. Small habitat islands are inferior breeding habitats bur are used by some Great tits - competition or ignorance? Biodivers. Conserv. 12, 1467–1479. doi: 10.1023/A:1023629810919
- MacDonald, E.C., Camfield, A.F., Jankowski, J.E., Martin, K., 2014. An alpine-breeding songbird can adjust dawn incubation rhythms to annual thermal regimes. The Awk 131, 495–506. doi: 10.1642/AUK-13-234.1
- Martin, T.E., 1987. Food as a limit for breeding birds: a life- history perspective. A. Rev. Ecol. Syst. 18, 453–487. doi: 10.1146/annurev.es.18.110187.002321
- Martin, T.E., 1995. Avian life history evolution in relation to nest sites, nest predation, and food. Ecol. Monograph. 65, 101–127. doi: 10.2307/2937160

- Matthysen, E., Adriansen, F., Dhont, A., 2011. Multiple responses to increasing spring temperatures in the breeding cycle of blue and great tits (*Cyanistes caeruleus, Parus major*) Glob. Change Biol. 17, 1–16. doi: 10.1111/j.1365-2486.2010.02213.x

- McNamara, J.M., Houston, A.L., 1990. The value of fat reserves and the tradeoff between starvation and predation. Acta Biotheoretica 38, 37–61. doi: 10.1007/BF00047272

- Moller, A.P., 1987. Breeding birds in habitat patches: random distribution of species and individuals? J. Biogeogr. 14, 225–236. doi: 10.2307/2844893

- Moller, A.P., 1991. Clutch size, nest predation, and distribution of avian unequal competitors in a patchy environment. Ecology 72, 1336–1349. doi: 10.2307/1941106

- Naef-Daenzer, B., Keller, L.F., 1999. The foraging performance of great and blue tits (*Parus major* and *P. caeruleus*) in relation to caterpillar development, and its consequences for nestling growth and fledging weight. J Anim. Ecol. 68, 708–718. doi: 10.1046/j.1365-2656.1999.00318.x

- Naef-Daenzer, B., Widmer, F., Nuber, M., 2001. Differential post fledging survival in Great and Coal tits in relation to their condition and fledging date. J. Anim. Ecol. 70, 730–738. doi: 10.1046/j.0021-8790.2001.00533.x

- Nagy, L.R., Stanculescu, D., Holmes, R.T., 2007. Mass loss by breeding female songbirds: food supplementation supports energetic stress hypothesis in Black-

659 throated Blue Warblers. The Condor 109, 304–311. doi: 10.1650/0010-
660 5422(2007)109[304:MLBBFS]2.0.CO;2
661 - Neto, J.M., Gosler, A.G., 2010. Variation in body condition of breeding Savi's
662 Warblers *Locustella luscinioides*: the reproductive stress and flight adaptation
663 hypothesis revisited. J. Ornithol. 151, 201–210. doi: 10.1007/s10336-009-0444-9
664 - Newton, I., 1994. The role of nest sites in limiting the numbers of hole-nesting
665 birds: a review. Biol. Conserv. 70, 265–276. doi: 10.1016/0006-3207(94)90172-4
666 - Nour, N., Currie, D., Matthysen, E., Van Damme, R., Dhont, A.A., 1998. Effects of
667 habitat fragmentation on provisioning rates, diet and breeding success in two
668 species of tit (great tit and blue tit). Oecologia 114, 522–530. doi:
669 10.1007/s004420050476
670 - Paton, P.W.C., 1995. The Effect of Edge on Avian Nest Success: How Strong Is the
671 Evidence? Conserv. Biol. 8, 17–26. doi: 10.1046/j.1523-1739.1994.08010017.x
672 - Perrins, C.M., 1965. Population fluctuations and clutch size in the Great tit, *Parus*
673 *major* L. J. Anim. Ecol. 34, 601–647. doi: 10.2307/2453
674 - Perrins, C.M., 1991. Tits and their caterpillar food supply. Ibis 133, 49–54. doi:
675 10.1111/j.1474-919X.1991.tb07668.x
676 - R Core Team., 2014. R: A language and environment for statistical computing. R
677 Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-
678 project.org/

679 - Razeng, E., Watson, D.M., 2014. Nutritional composition of the preferred prey of
680 insectivorous birds: popularity reflects quality. J. Avian Biol. 45, 001–008. doi:
681 10.1111/jav.00475

682 - Riddington, R., Gosler, A.G., 1995. Differences in reproductive success and
683 parental qualities between habitats in the Great Tit *Parus major*. Ibis 137, 371–378.
684 doi: 10.1111/j.1474-919X.1995.tb08035.x

685 - Robinson, S.K., Thompson, F.R., Donovan, T.M., Whitehead, T.R., Faaborg, J.,
686 1995. Regional forest fragmentation and nesting success on migratory birds.
687 Science 267, 1987–1990. doi: 10.1126/science.267.5206.1987

688 - Robles, H., Ciudad, C., Matthysen, E., 2012. Responses to experimental reduction
689 and increase of cavities by a secondary cavity-nesting bird community in cavity-rich
690 Pyrenean oak forests. Forest. Ecol. Manage. 27, 746–53.
691 doi:10.1016/j.foreco.2012.04.017

692 - Salvador, A., Pleguezuelos, J.M., 2002. Reptiles Españoles. Identificación, historia
693 natural y distribución. In Sfagnos. Canseco Editores S.L. Talavera de la Reina,
694 Toledo.

695 - Shochat, E., Abramsky, Z., Pinshow, B., 2001. Breeding bird species diversity in
696 the Negev: effects of scrub fragmentation by planted forests. J. Appl. Ecol. 38,
697 1135–1147. doi: 10.1046/j.1365-2664.2001.00667.x

- Stahl, J., Tolsma, P.H., Loonen, M.J., Drent, R.H., 2001. Subordinates explore but dominants profit: resource competition in high Arctic barnacle goose flocks. Anim. Behav. 61, 257–264. doi:10.1006/anbe.2000.1564
- Svensson, E., Nilsson, J.A., 1995. Food supply, territory quality, and reproductive timing in the Blue tit (*Parus Caeruleus*). Ecology 76, 1804–1812. doi: 10.2307/1940712
- Tinbergen, J.M., Boerlijst, M.C., 1990. Nestling weight and survival in individual Great tits *Parus major*. J. Anim. Ecol. 59, 1113–1127. doi: 10.2307/5035
- Tremblay, I., Thomas, D.W., Lambrechts, M.M., Blondel, J., Perret, P., 2003. Variation in blue tit breeding performance across gradients in habitat richness. Ecology 84, 3033–3043. doi: 10.1890/02-0663
- Tremblay, I., Thomas, D., Blondel, J., Perret, P., Lambrechts, M.M., 2005. The effect of habitat quality on foraging patterns, provisioning rate and nestling growth in Corsican Blue tit *Cyanistes Caeruleus*. Ibis 147, 17–24. doi: 10.1111/j.1474-919x.2004.00312.x
- Van Noordwijk, A.J., McCleery, R.H., Perrins, C.M., 1995. Selection for the timing of Great Tit breeding in relation to caterpillar growth and temperature. J. Anim. Ecol. 64, 451–458. doi: 10.2307/5648
- Van Noordwijk, A.J., van Balen, J.H., Scharloo, W., 1988. Heritability of body size in a natural population of Great tit (*Parus major*) and its relation to age and environmental conditions during growth. Genet. Res. 51, 149–162. doi: 10.1017/S0016672300024162

- Verhulst, S., Perrins, C.M., Riddington, R., 1997. Natal dispersal of Great tits in a patchy environment. Ecology 78, 864–872. doi: 10.2307/2266065
- Visser, M.E., Holleman, L.J.M., 2001 Warmer springs disrupt the synchrony of oak and winter moth phenology. Proc. R. Soc. Lond. Ser. B Biol. Sci. 268, 289–294. doi: 10.1098/rspb.2000.1363
- Visser, M.E., Holleman, L.J.M., Gienapp, P., 2006. Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. Oecologia 147, 164–172. doi: 10.1007/s00442-005-0299-6
- Zanette, L., Doyle, P., Trémont, S.M., 2000. Food shortage in small fragments: Evidence from an area-sensitive passerine. Ecology 81, 1654–1666. doi: 10.2307/177314
- Zitsque, B.P., Betts, M.G., Diamond, A.W., 2011. Negative effects of habitat loss on Survival of Migrant Warblers in a Forest Mosaic. Conserv. Biol. 25, 993–1001. doi: 10.1111/j.1523-1739.2011.01709.x
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Series: Statistics for Biology and Health. Ed. Springer, NY.